A STUDY OF THE VEGETATIVE ANATOMY OF THE GENUS SPHENOPHYLLUM FROM AMERICAN COAL BALLS

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INTRODUCTION

Although the genus *Sphenophyllum* has been described in some of the earliest paleobotanical works and Seward (1898) lists it as one of the best-known fossil plants, the rich source of petrified specimens in the American coal balls has been very largely ignored. The works of Renault and Williamson (1878) did much to make known the inner structure of the stems, roots and leaves of the English and European forms, although gaps were left concerning our knowledge of branching, the attachment of roots, and other anatomical points. It was with the hope, therefore, of contributing to our knowledge of the internal structure of the plants, as well as the desire to make better known the American fossils and to correlate them in so far as possible with the English and French species, that this study was undertaken.

The material on which this study was based was obtained from two sources as follows: The Pyramid mine, two miles south of Pinckneyville, Perry County, Illinois, this horizon being at the base of the McLeansboro series (coal No. 6) and of upper-middle Pennsylvanian age; and The What Cheer Clay Products Co. coal mine, one-half mile west of What Cheer, Iowa. This horizon lies in the Des Moines series of the Pennsylvanian.

REVIEW OF LITERATURE

Sphenophyllum, in the form of compressions, has been noted and described by some of the earliest investigators. Solms-Laubach (1891) states, "The genus, owing to its striking appearance, has been repeatedly figured by the old authors." In Scheuchzer's *Herbarium Diluvianum* (1723) there are drawings of stem fragments bearing whorls of small wedge-shaped leaves which were undoubtedly made from specimens of *Sphenophyllum.*

Renault (1878) was the first to link together definitely the petrifactions showing internal anatomy with the well-known leaf and stem compressions. He described three species from petrified material, only one of which, S. *quadrifidum,* has been retained by recent authors. It is supposedly characterized by double groups of protoxylem at each angle of the primary triangle, giving a hexarch structure. However, in examining Renault's original plates and descriptions we have found little evidence of clearly defined hexarch anatomy. His other two species based on petrifactions were S. *stephenense,* which is figured as having two forked and two single leaf traces from each protoxylem angle, and S. *erosum,* which his drawing purports to show with 18 leaf traces radiating out from the stele in all directions. Whatever the 18 "rays" were in the later drawing, we feel certain that they were not leaf traces though it is possible that they could have been vascular strands to adventitious roots.

Williamson (1874) described two petrified stems with triarch protosteles as species of *Asterophyllites*. In 1895, recognizing their true nature, he redescribed them in detail and with many excellent illustrations, as *Sphenophyllum plurifoliatum* and *Sphenophyllum insigne*. *S. plurifoliatum* did not differ in any important anatomical features from the specimens previously figured by Renault, but Williamson's detailed descriptions clarified the characteristic structure of the genus. *S. insigne* differed in coming from a much lower horizon in the Lowest Carboniferous, supposedly in having fairly consistent continuous parenchyma rays in the interfascicular[1] wood, and in the presence of protoxylem lacunae.

Koopmans (1928) has described two new species, *S. minus* and *S. perforatum*, from the Finefrau horizon of the Netherlands. The former differs from *S. plurifoliatum* in having a smaller protoxylem strand (0.4 mm.), a less concave metaxylem, a narrower fan of fascicular xylem, and smaller interfascicular xylem cells adjoining the metaxylem. *S. perforatum* differs in possessing protoxylem lacunae, smaller metaxylem cells, and more prominent arms to the primary wood triangle. We shall have more to say concerning these species later.

Leclercq (1925) has described *S. Gilkineti* from the upper Carboniferous of Belgium on the basis of two different zones of secondary wood. This species will be treated more fully below when variations of the *Sphenophyllum* stem are described.

With the exception of the six species just mentioned, all of the other *Sphenophyllum* species have been described on the basis of leaf differences observable in compressions. Potonié (1910) lists eight species, while Lesquereux (1880), in his work on the coal flora of Pennsylvania, describes nine variations in leaf form. Five of these he assigns to European species, intimating a close relationship for the plant in the two geographical areas, a fact which finds support in petrified material. Indeed Walton (1940) illustrates (his figure 42) a *S. plurifoliatum* stem type from England which is so similar to the Illinois material that it could have been made from one of our own peels.

Prior to this study there has been almost no attention paid to petrifactions of *Sphenophyllum* in this country. A few investigators have mentioned finding stems of the *S. plurifoliatum* type in American coal balls but no descriptions have been given. Darrah (1939), in dealing with the flora of Iowa coal balls, listed *Sphenophyllum* stems and strobili (of the *S. Dawsoni* type) but did not include any illustrations or descriptions. This neglect is the more surprising since the Iowa and Illinois coal balls contain abundant and excellent specimens. It is a rare coal ball that does not produce at least one or two stems, while some are found with as

[1] The terms fascicular and interfascicular are used here and throughout the text in the sense originated by Williamson and Scott (1895): fascicular, in all cases, referring to that secondary wood formed opposite the protoxylem groups; and interfascicular indicating the secondary tissue formed opposite the sides of the triangular protostele and between the protoxylem groups.

many as nine or ten stems in an area 3–4 inches in diameter. Consequently we have had the advantage of being able to observe hundreds of specimens in varying stages of growth.

General Description

The external appearance, as evidenced in compressions, is that of a slender stem 1 cm. or less in diameter, with cortical furrows and whorls of leaves which do not alternate from node to node as in *Calamites*. (The most ancient of the *Calamites*, *Archaeocalamites*, from the Lower Carboniferous did, however, have the same superimposed structures.) The nodes themselves are commonly somewhat swollen while the leaves vary considerably in size and form, a large number of species having been described on the basis of foliar differences. The type on which the genus was founded has wedge-shaped leaves with an entire or very slightly toothed margin. In some species the foliage is deeply dissected, while in others the plants are heterophyllous, bearing both entire and deeply lobed leaves on the same stem. The anatomy of the stem has constituted one of the primary reasons for the isolation of the genus.

Primary Tissues

Transverse sections of the stems show the primary wood to be a solid mass of tracheids, triangular in outline and with the protoxylem occupying the apices of the triangle. The protoxylem tracheids are small (20 μ in diameter), with ring or spiral thickening. The transition to metaxylem is quite abrupt, with a distinct increase in cell size and a characteristic reticulate bordered pitting on both the radial and tangential walls.

Generally most of the plants observed appear to comply with the descriptions of *Sphenophyllum plurifoliatum* Williamson. However, we shall point out several variations from the basic *plurifoliatum* type which seem to indicate that stem anatomy, at least in the internodal region, may constitute a doubtful basis for specific differences.

On the whole, our Illinois specimens are smaller than those described from England and Europe. The largest stem observed was not over 4 mm. in diameter, while Williamson (1895) has indicated that many of the English specimens reached 1 cm. It is of some interest also to note that while Bower (1930) observed primary wood averaging 1 mm. in width (measured from a protoxylem angle across to the opposite fascicular wood) the largest we have been able to secure measures .5 mm., the average size being .4 mm. The Iowa stems (figs, 3, 7, 8, 10 and 11) show the same small primary wood, though some of them (figs. 7, 11) exhibit considerably more secondary wood with larger total diameter than was found in the Illinois specimens.

Immediately adjoining the primary wood there is often a layer, usually one cell thick but sometimes two, of xylem parenchyma which surrounds the entire triangle with the exception of the protoxylem angles (fig. 17).

Figure 1 illustrates a stem which presents the features of S. *plurifoliatum* although showing clearly defined protoxylary canals which hitherto have been observed only in the more ancient S. *insigne*.

The lacunae appear to be the result of a disintegration of the protoxylem tissues, as very often an accompanying disruption is to be noted in the adjoining fascicular wood. From the constancy of their occurrence there is little doubt but that they represented a character of the living plant. Figure 1, showing one of the few stems of this type retaining its epidermis (most of the specimens having only a thick periderm), exhibits deeper and more numerous furrows (in this case eight) than are usual in S. *plurifoliatum*, which commonly has just three deep grooves opposite the sides of the primary triangle. However, none of these specimens just described was found with leaves or branches, and because our studies on the external form of the stem at the node and internode in a definite S. *plurifoliatum* stem showed that there could be very wide differences in size and form it seems wiser, at least for the present, to list this group as one of the variations of the basic *plurifoliatum* type than to attempt to assign it specific value.

Secondary Tissues

The secondary wood is radially arranged around the triangular primary tissues in a geometrical pattern that results in the rows of cells opposite the protoxylems being much smaller than those opposite the metaxylem. Consequently the fascicular wood forms a radiating fan of narrow rows of small cells which gradually increase as their angle of divergence increases until in the outer margin of large stems the two zones are almost identical (fig. 11). According to Williamson (1895) and Scott (1920), this fascicular region has continuous parenchyma rays of a different type from those of the interfascicular wood. However, we have been unable to observe any evidence of this in our material, while indeed some stems (fig. 11) very obviously show identical ray structure to the interfascicular zone.

The tracheids of the interfascicular xylem are in transverse section normally large, rectangular, and with truncated angles, the spaces between them being occupied by groups of small, vertically aligned parenchymatous cells. In radial section these vertical parenchyma cells are connected by many small horizontal ones extending across individual tracheids, forming an effective ray system (fig. 8).

Figures 5 and 6 show an interesting stem in which an injury evidently caused the growth of "fascicular type" wood for over two-thirds of the circumference. The injury appears to have occurred when two rows of secondary wood had been formed and to have caused the cambium to start producing a series of smaller cells. On the side of the stem farthest from the wounding the secondary wood was unaffected. The abnormality is evidently quite similar to *Sphenophyllum Gilkineti* Leclercq, concerning which we shall say more later.

Another secondary wood variant is illustrated in fig. 2. Here an apparent sclerotic growth is seen replacing the usual corner groups of parenchyma. The

Sphenophyllum nature, however, is still obvious in the triarch structure of the primary wood, the deep-seated periderm, and the sclerotic furrowed outer cortex.

The pitting of the secondary wood is similar to that described for the metaxylem except that there are fewer pits in the tangential walls. The pitting presents a good character for recognizing the genus in longitudinal sections, the pits being ovoid to circular and arranged so thickly on the radial walls that they form a reticulate pattern. All previous investigators have described these pits as bordered, but it seems likely that the border must have been quite fragile, since the pits normally appear simply as perforations in the cell wall (fig. 8). Next to the pitting the most distinctive character of the wood is the length of the xylem cells. Although longitudinal sections over 1 cm. long were obtained, it was still impossible to find any trace of end walls, so the question of the true nature of these cells (tracheids or vessels) must remain an open one.

The parenchyma tissues outside the wood are seldom well preserved, being replaced at an early stage by a deep-seated periderm which appears to have arisen first in the pericycle or endodermis and then in successively deeper series within the phloem. Figure 12 illustrates a cross-section showing two layers of periderm, the inner abutting almost directly on the secondary wood so that only a few fragments of phloem and cambium remain. In longitudinal view the periderm can be seen to consist of regular rows of short parenchymatous cells, darker in color than the other stem tissues and appearing to retain considerable cell contents.

The outer cortex in mature stems is often replaced by the thick periderm growths just described. When present it offers a distinctive character in its strongly sclerotic appearance and furrowed outline.

Branching

To our knowledge, branching in the petrified material of *Sphenophyllum* has not been reported up to this time. Williamson (1874) illustrated a specimen showing the base of a lateral appendage, although it seems most likely that it represented a root departure. The vascular tissue followed a horizontal course outward from the stele which, as will be pointed out, appears to be characteristic of the leaves and roots but not of true branches. It was with particular interest, therefore, that we found in the specimens represented in the Illinois and Iowa coal balls three stems exhibiting clearly defined branching, each quite different and distinct.

The first stem to be described is characterized in the internode by the roughly hexagonal shape of the outer cortex and an oval periderm surrounding the triangular woody tissue (fig. 15). As the node is approached both the outer cortex and the inner parenchyma layers immediately surrounding the xylem become almost spherical (fig. 16). A short distance above this the general form molds itself to that of the woody cylinder and becomes triangular throughout (fig. 18). At this stage the first evidence of branching is seen in the out-thrusting of segments of pericycle and phloem tissue through the surrounding periderm and cortex at points opposite the protoxylem angles. There also appear at this time swellings in the periderm, approximately along side of each of the three protoxylem groups, two of them on each side of the triangle. Next, the over-all shape of the stem becomes more definitely triangular and horizontal vascular strands appear extending out from the protoxylem into the three corners and also into the six swellings on the sides (fig. 19). In the next peel (fig. 20) we see that the six side vascular strands lead into the bases of leaves while the fascicular tissues at the corners have extended through the outer cortex at a sufficient angle from the horizontal to exhibit most of their area in transverse view. These large corner vascular bundles, surrounded by a thin layer of phloem and pericycle and what appears to be tissue from the periderm, are soon pushed out beyond the outer cortex of the main stem. At this stage adventitious roots are produced abundantly and appear passing out through the cortex of these vascular bundles in all directions (figs. 20 and 22). The following stage finds the three branches separated from the main stem by their own sclerotic outer cortex. The numerous adventitious roots are still evident while the stem is observed to have regained its original hexagonal form (fig. 21). Our last illustration of this series shows the central portion of one of the branches, some distance from the main stem, in which the characteristic triarch stele structure is beginning to appear (fig. 23).

In the second specimen the stem produced just one branch instead of three, and there is no evidence of a node or leaves in the vicinity of the branching. The offshoot is first observed as a large mass of fascicular wood coming off from a protoxylem corner of the primary triangle. Its angle of departure from the stem is quite acute so that it maintains an approximate vertical position throughout its passage. The main stem, instead of the triangular shape characteristic of our other specimen, is a flattened oval with the elongation in the direction of the branching (fig. 26). The preservation of the branch was so very poor shortly after it became independent that it was not possible to follow it for a sufficient distance to show a node; however, fig. 27 illustrates its appearance at the point of separation from the stem. The typical sclerotic furrowed outer cortex is evident, and while the primary wood does not as yet exhibit the usual triangular form of our previous specimen (in which the preservation was considerably better) this character did not develop until some distance from the main stem. Probably the most curious feature of this specimen is the production of two curved appendages from the other two corners of the primary triangle at the same vertical position as the start of the branch trace (fig. 25). The vascular tissue in these appendages is horizontal (90° angle to the main stem) and the structures themselves are apparent for some distance in a horizontal position. They are quite small and with a thick cortex, at least at the base where they depart from the stem, so they obviously could not be leaves. We are, therefore, inclined to regard them as modified roots which functioned as specialized appendages enabling the vine-like *Sphenophyllum* to cling or prop itself upon supporting surfaces.

The third form of branching observed is illustrated in figs. 7 and 10 and appears to have consisted of an unequal dichotomy with the branch being considerably larger than the main axis. That the larger structure constituted the branch was proved by longitudinal sections showing the angle of departure. This feature would seem to offer additional evidence of the vine-like nature of *Sphenophyllum*.

Leaves

The leaves were borne in whorls at the nodes and were fused for a short distance from the base (fig. 29). They were in multiples of three, and six appears to be the average number of the Illinois and Iowa specimens. In the six-leaved specimens vascular tissue was supplied by means of V-shaped traces given off from each angle of the primary triangle, one trace going into each leaf and dividing dichotomously in the outer cortex or the leaf base. Figure 3 shows an unusually perfect nodal section with all six leaf traces traversing the cortex into the leaf bases. In the destruction of the inner tissues the connection of the traces to the protoxylem angles has been lost; however, fig. 32, a nodal section of a smaller stem, comes fairly close to showing the attachment.

The internal anatomy of the leaf appears to have been relatively simple. The outstanding feature in the petrified material is the conspicuous ring of fiber strands enclosing the 7–8 tracheids which form the vein (fig. 24). The mesophyll seems to have been undifferentiated and seldom of more than one or two cells in thickness. The lower and upper epidermal layers were one cell thick and with no apparent cuticle. No stomata were observed though they have been reported by Renault (1878).

Roots

The roots were first identified and investigated by Renault (1878). The identification was made on the basis of relatively large roots which possessed the same distinctive secondary wood as the stems. Since then they have been noted and figured by various investigators but never organically connected with the stems.

Early in the present work it was noticed that surrounding many of the *Sphenophyllum* stems were small roots averaging .3 mm. to .4 mm. in diameter. These consisted of 2–7 small tracheids, a well-defined endodermis, 2–3 layers of large parenchymatous cortex cells (average diameter 50 μ), surrounded by a single-layered epidermis of conspicuously large cells (diameter 40 μ), with abundant root hairs (figs. 9 and 30). From two coal balls we were able to secure peels which contained, along with the *Sphenophyllum* stems, almost homogenous masses of these roots in which all sizes were represented from the smallest, described above, to mature roots such as illustrated in fig. 28. These showed a nearly continuous series of developmental stages, indicating conclusively that these small previously undescribed roots represent the initial stage of the already known mature specimens. Secondary growth appears to have been initiated very early and to have produced rapidly the characteristic square tracheids with the groups of parenchyma cells at their angles. Since the cambial growth was from a small rounded primary strand the radiating rows of secondary wood are uniform and are not differentiated into fascicular and interfascicular zones as in the stem where the growth was from a triangular base. A phellogen also became active in the endodermis at an early stage and by the time that 4–5 layers of secondary wood had been produced the periderm had usually grown to the degree that the cortex and epidermis were lost. Thus these latter tissues are observable only in the youngest roots (fig. 30).

In none of our specimens do we find much support for the belief that these roots were diarch or even monarch in the strict sense. Figure 30 illustrates a small root in which there are approximately six tracheids composing the primary wood. There is no apparent growth of metaxylem, while there does seem to be, even at this early stage, the initiation of secondary growth as evidenced by the large tracheids to be seen on both sides of the primary tissue.

In order to establish beyond any doubt the *Sphenophyllum* origin of these roots particular attention was paid to finding some in actual connection with the stems. In making a longitudinal series of peels through a well-preserved specimen, the structure illustrated in fig. 35 was discovered. Here we have a root identical to the small ones described above, within the middle cortex of a *Sphenophyllum* stem. The conspicuous epidermis, large cortical cells, and dark endodermis are clearly recognizable. The evidence seems to be quite definite that the adventitious growth of these roots could and did occur on any part of the stem but that it was ordinarily most abundant in the vicinity of the nodes. As previously mentioned in the description of branching, many of these small roots were observed being given off at the base of the newly formed branches (figs. 21 and 22).

In addition to the above instances, figs. 31 and 33 show a longitudinal section of a *Sphenophyllum* stem with what we believe to be extremely large roots being given off opposite each other and immediately dividing into groups of small roots. Figure 31 shows the vascular strand passing horizontally from the stem into the appendage. It is felt that this is an important diagnostic character since, as indicated earlier, the vascular bundles passing to the branches always leave the stele at an acute angle. Therefore only the leaves and the roots exhibit this horizontal passage of the vascular tissue, and in this case we are clearly not dealing with a leaf.

The pitting of the tracheids of both small and large roots was observed in longitudinal radial sections. The reticulate bordered pitting, so common on the radial walls of the stems, was clearly evident in both.

Discussion

It is apparent that although *Sphenophyllum* has been described as "one of the best-known fossil plants" (Williamson and Scott, 1895), and has been illustrated by numerous authors since Renault's time, there still remain phases of its general organization that need clarification.

Our three stems, while presenting identical anatomy in the internode region, show quite distinct differences at the point where the branch or branches are given off. In one we have three offshoots at a conspicuous node, while in another just a single branch is produced with root-like appendages springing from the other two protoxylem angles and with no sign whatever of any node or leaves, and in the third there is an unequal dichotomy with the branch being the larger. In all three the branch vascular tissue originates from the main stele at an acute angle instead of a right angle, as is characteristic of the leaves and roots, and the first two specimens described show typical sclerotic cortex; while the specimen in which we were able to follow the branch for some distance presented a clearly outlined triarch protostele. Therefore we have either the anomaly of three distinct branching patterns on one plant or significant taxonomic characters which are not correlated with any other observed differences in stem anatomy.

It would seem that the anatomy of the internode (which makes up 99 per cent of the sections usually obtained) is an unreliable key to specific segregation, in that it fails to emphasize sufficiently such differences as may exist in other parts of the plant, or may, on the other hand, present misleading supposedly specific differences. Examples of this latter point are illustrated in figs. 2 and 5 where the variations are, we feel, due to some local outside influence.

Further difficulty in attempting to define additional species on stem anatomy is well shown in the specimen illustrated in fig. 15. Here the internodal structure is identical in every way to S. *plurifoliatum* but at the node is shown clearly to have only six leaves, while both Scott (1920) and Williamson and Scott (1895) state repeatedly that their specimens had many leaves, probably around 18. Lacking nodal sections they could not make an exact count but evidently they had considerable evidence from leaf parts preserved with the stem. Possibly they were working with a different species than we have illustrated, but one of strikingly similar wood anatomy.

All points considered, it seems more feasible, at least for the present, to allow the species S. *plurifolium* as described by Williamson and Scott to cover nomenclature needs of these Illinois and Iowa petrified stems. We do feel that a short description of the structural variations is worth giving here. Then, if additional research reveals correlating characters in other plant organs they could be given specific importance.

Type 1.—Characterized by constant presence of protoxylem lacunae. Protostele averages .4 mm. from angle to opposite side of triangle. Large metaxylem cells with occasional xylem parenchyma on margin. Outer cortex in internode region more or less circular in outline with 8–10 deep furrows (fig. 1). This type resembles S. *perforatum* and S. *insigne* in its possession of protoxylem lacunae, but in all other respects it is identical to S. *plurifoliatum*. The characters separating the aforesaid species from S. *plurifoliatum* are, in our opinion, doubtful.

In examination of Williamson's figures and of *Sphenophyllum insigne* peels from the Calciferous Sandstone horizon we have been unable to observe the continuous medullary rays in the interfascicular wood. This feature, along with the protoxylem lacunae, supposedly distinguished the species, while the slight differences in size and form of the primary wood listed by Koopmans for S. *perforatum*, in our opinion, are too variable to be reliable.

Type 2.—No protoxylem lacunae. Definite xylem parenchyma between metaxylem and interfascicular wood. Large metaxylem cells, equal in size or larger than secondary wood. Protostele size averages same as above. External form of outer cortex at the internode is hexagonal with a deep furrow opposite each side of triangular protostele. S. *minus* Koopmans would fall in this group. The differences in the concavity of the metaxylem, shape and size of the fascicular and interfascicular wood are not, we feel, constant enough in any of the forms to be reliable characters. The pure size difference of the protoxylem that has been observed in the Netherlands and Illinois and Iowa forms is not in itself sufficient reason for separating them from S. *plurifoliatum*.

Type 3.—Abnormal growths resulting from injury to stem (figs. 5 and 6) and sclerotic growths replacing usual corner parenchyma (fig. 2). Not really types at all but specimens which may show up with some frequency and which should be recognized for what they are. S. *Gilkineti* is, we feel, identical to the type showing abnormal growth resulting from wounding. Miss Leclercq's type specimen, as she stated, also had obviously been injured in growth and while she recognized the possibility of its being an abnormal growth her reasons for assigning specific value were as follows:

> Nous avons longtemps hésité dans l'interprétation des nos échantillons des figures 2 et 3. La présence de deux bois secondaires différents dans la tige complète de la figure 2 pouvait elle s'expliquer uniquement par l'excitation des tissus végétaux due aux buessures, ou représentait-elle la structure normale d'un nouveau type de *Sphenophyllum?* [p. 33].
>
> La découverte, dans le travail de Williamson, d'une coupe transversale très bien conserveé, d'un *Sphenophyllum* identique à celui de notre figure 2, a levé le doute quant à l'interprétation; nous sommes bien en présence d'une espèce nouvelle. Il est en effet invraisemblable de supposer que le *Sphenophyllum* de Williamson ait pu etre blessé lui aussi de telle manière qu'il reproduise une structure identique à celle de notre S. *Gilkineti.* [p. 33].

With our discovery of a stem showing the two zones of secondary wood accompanied by wounding it no longer seems "improbable" to suppose that Williamson's figure was also of an injured stem.

There is still much to be learned from more extensive studies of the petrifactions of *Sphenophyllum*. It is undoubtedly a larger group and more diversified than has been so far suspected. While the anatomy of the internode seems unreliable as a basis for specific distinctions (at least from the present material) the discoveries of additional nodal sections may be expected to show wide variations in leaf and branch form of possible specific value

The most important implications, we believe, to come out of the present study are additional facts for the relationship of *Sphenophyllum* to Equisitales. As Jeffrey (1899) points out "protostely and siphonostely may occur in different genera of the same family, and even different species of the same genus." So with the observance in *Sphenophyllum* of fairly common protoxylem lacunae and origin of the branches *between* the leaves the only major distinction separating the groups is the peculiar parenchyma ray system of *Sphenophyllum*, and in this we have seen how occasional horizontal conjunction of the radiate parenchyma may produce structures similar to normal rays.

Therefore, on the basis of vegetative anatomy, we are inclined to agree with Jeffrey that there is no valid reason from excluding *Sphenophyllum* from the Equisitales and that it should be regarded as an offshoot from the group ancestor in which the primitive protostele and superimposed internode and leaf whorls have been retained.

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Explanation of Plate

PLATE 12

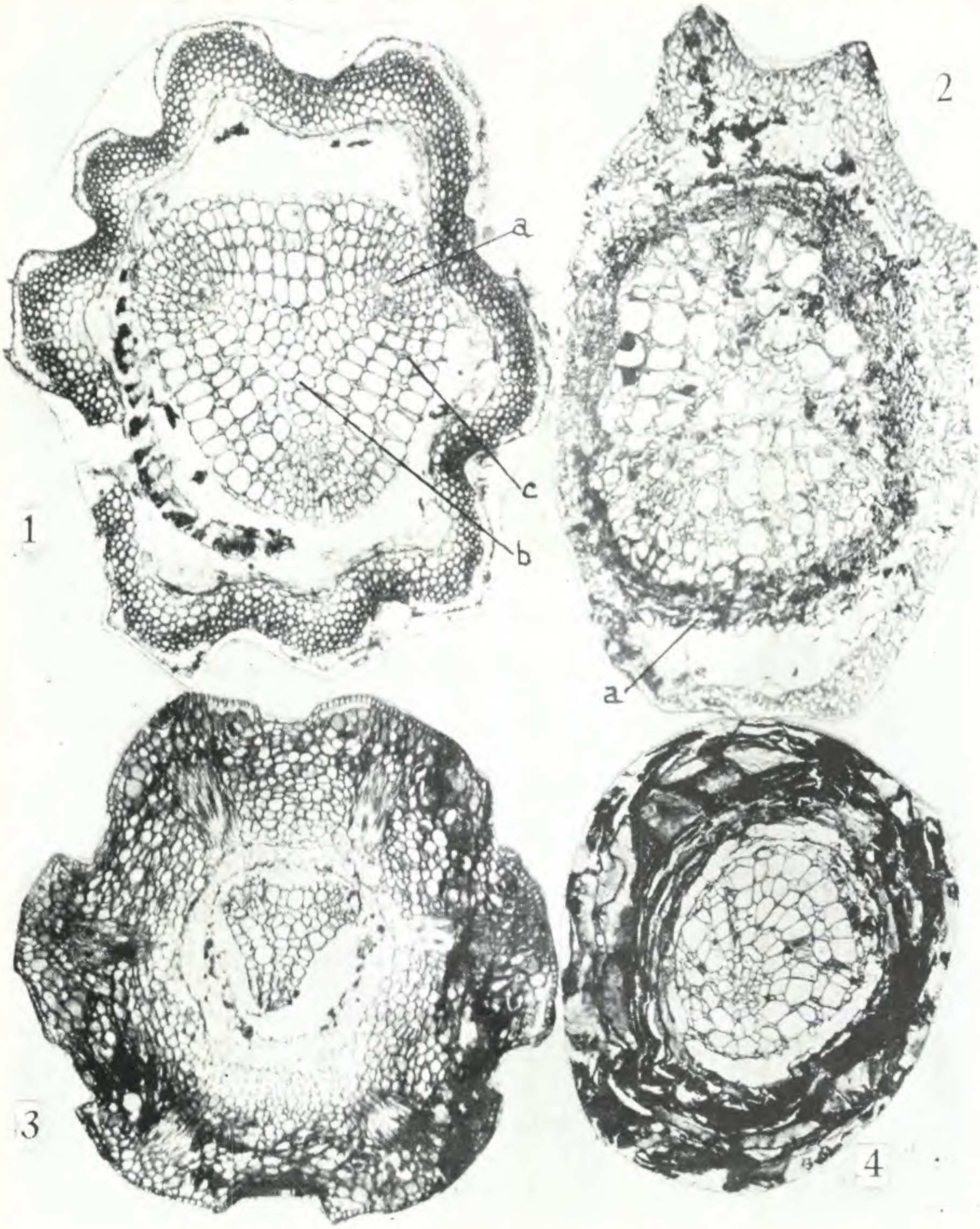
Sphenophyllum plurifoliatum

Fig. 1. Transverse section of stem showing eight cortical furrows: *a*, protoxylem lacuna; *b*, metaxylem; *c*, parenchyma ray extending through three rows of secondary wood. From slide 1523, × 17.

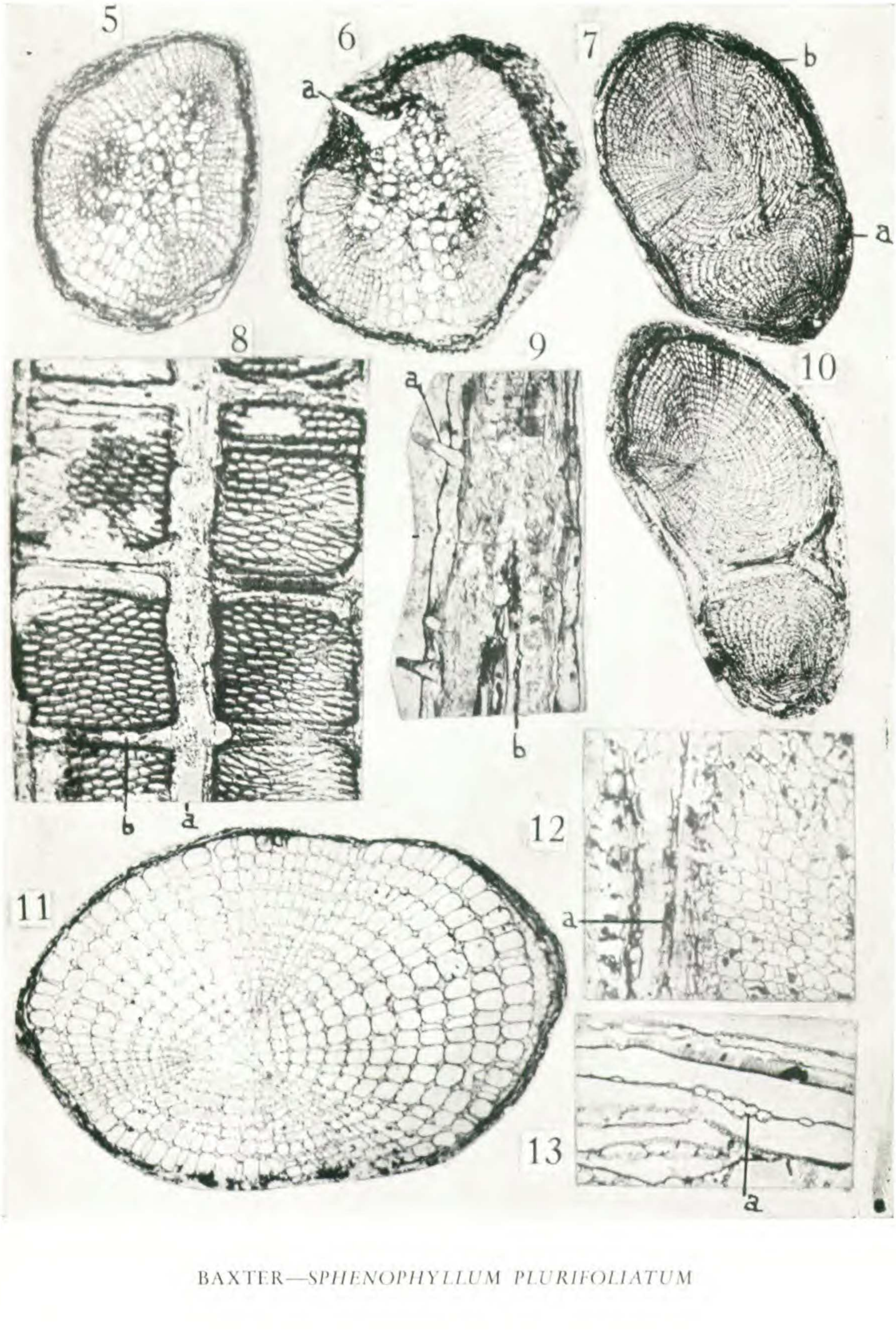
Fig. 2. Transverse section of stem showing sclerotic type of stele: *a*, internal periderm. From slide 1524, × 34.

Fig. 3. Transverse section of a stem at the node showing all six leaf traces passing into the leaf bases. From slide 1525, × 15.

Fig. 4. Transverse section of a medium-sized root showing thick periderm layer. Secondary wood unevenly developed. From slide 1526, × 60.



BAXTER—*SPHENOPHYLLUM PLURIFOLIATUM*



BAXTER—*SPHENOPHYLLUM PLURIFOLIATUM*

Explanation of Plate

PLATE 13

Sphenophyllum plurifoliatum

Fig. 5. Transverse section of stem showing two zones of secondary wood on two sides of the primary wood triangle with normal development on the third side. From slide 1527, × 17.

Fig. 6. Transverse section of same stem as in fig. 5 at a slightly different level showing wounding of the tissues at the point of origin of the second zone of different growth. From slide 1528, × 17.

Fig. 7. Transverse section of a stem showing unequal dichotomy: *a*, main axis; *b*, branch. From slide 1529, × 4.

Fig. 8. Longitudinal-radial section of two rows of inter-fascicular tracheids (vessels?) showing characteristic reticulate pitting: *a*, area occupied by vertical parenchyma cells; *b*, one of horizontal-radiate parenchyma cells. From slide 1530, × 85.

Fig. 9. Longitudinal section of small *Sphenophyllum* root: *a*, root hair; *b*, endodermis. From slide 1526, × 45.

Fig. 10. Same stem as in fig. 7. Forking of stem almost complete; orientation same as above. From slide 1531, × 4.

Fig. 11. Transverse section of a stem with approximately twelve rows of secondary wood radiating out from the central triangular protostele. Note that interfascicular and fascicular wood are identical towards outer margin. Ray structure uniform throughout. From slide 1532, × 11.

Fig. 12. Transverse section of a portion of stem showing interfascicular wood, cambium and two layers of periderm: *a*, inner periderm. From slide 1533, × 22.

Fig. 13. Longitudinal-tangential view of secondary wood: *a*, horizontal-radiate ray approximately six cells deep. From slide 1534, × 60.

Explanation of Plate

PLATE 14

Sphenophyllum plurifoliatum

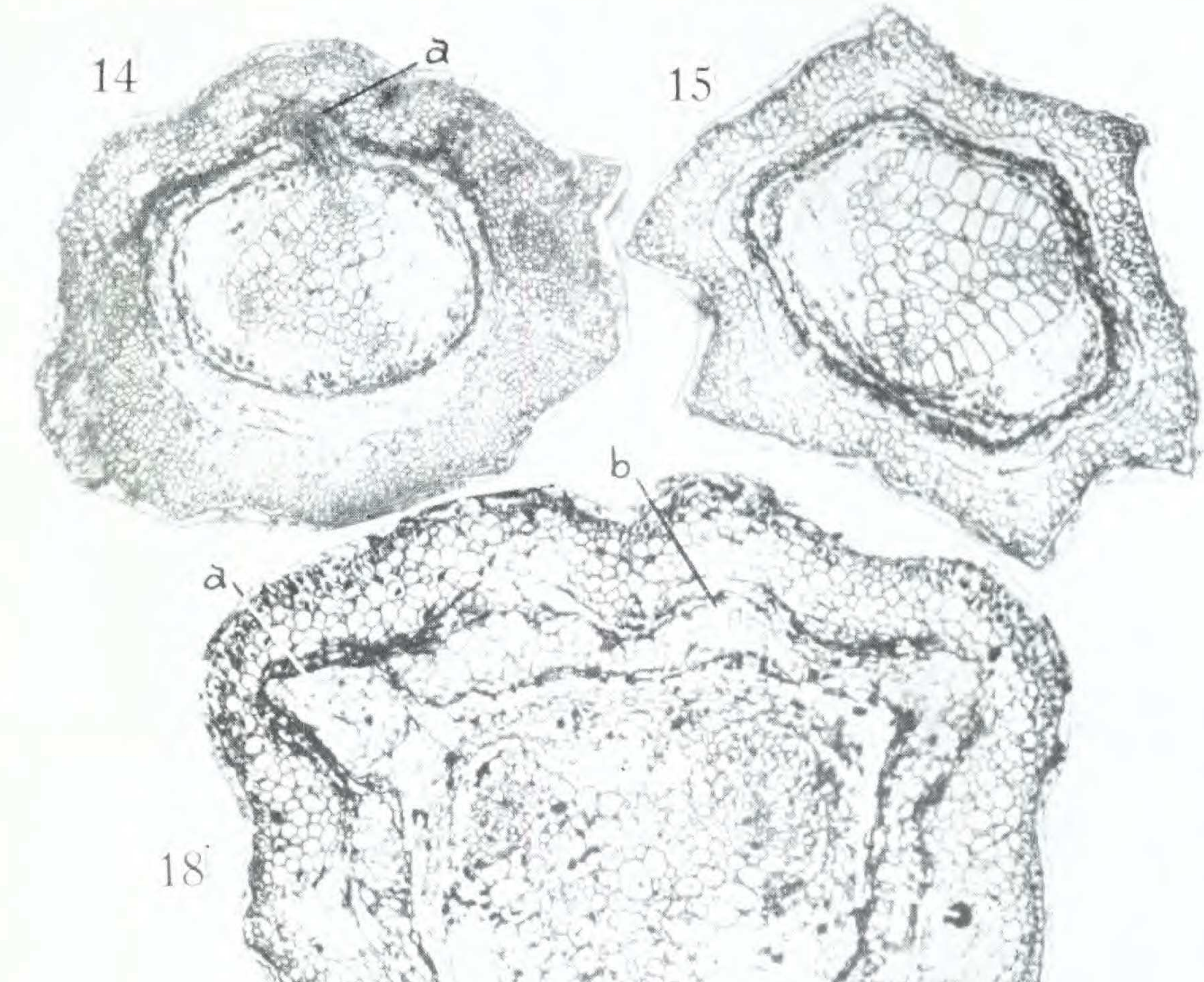
Fig. 14. Transverse section of stem in region of the internode showing production of adventitious root: *a*, adventitious root arising from protoxylem. From slide 1535, × 18.

Fig. 15. Transverse section of same stem as in fig. 14 showing characteristic hexagonal shape. From slide 1536, × 18.

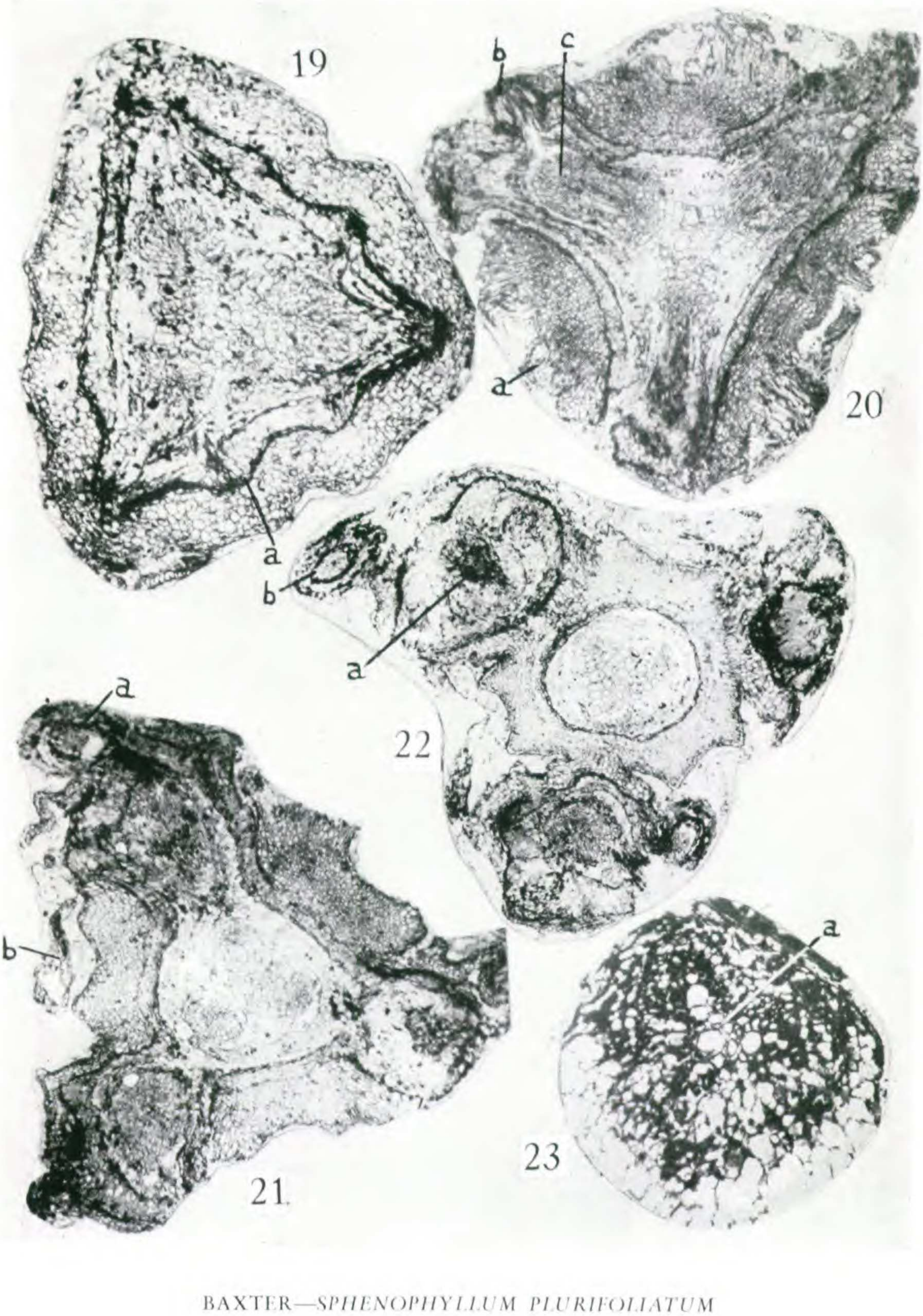
Fig. 16. Same stem as above, with section approaching the node. Note rounded outline and clearly defined cortical furrows opposite interfascicular wood. From slide 1537, × 18.

Fig. 17. Enlargement of the stele of preceding figure: *a*, secondary wood; *b*, protoxylem. From slide 1537, × 60.

Fig. 18. Same stem as above, transverse section at lower edge of the node: *a*, adventitious root preceding branch; *b*, swelling in periderm at position of trace to a side leaf. From slide 1538, × 24.



BAXTER—*SPHENOPHYLLUM PLURIFOLIATUM*



BAXTER—*SPHENOPHYLLUM PLURIFOLIATUM*

Explanation of Plate

PLATE 15

Sphenophyllum plurifoliatum

Fig. 19. Same stem as in fig. 18, showing a section slightly nearer the center of the node: *a*, trace to one of six side leaves. From slide 1539, × 12.

Fig. 20. Continuing nodal series in same stem: *a*, leaf base of one of six side leaves; *b*, adventitious root; *c*, vascular bundle to branch. From slide 1537, × 12.

Fig. 21. Same stem as above; vascular bundles to branches have become separated from main stele: *a*, adventitious root shown in fig. 20 *(b)*: *b*, segment of one of six side leaves. From slide 1540, × 12.

Fig. 22. Continuing nodal series in same stem, showing whorl of three branches almost free from the main stem: *a*, triangular primary wood; *b*, adventitious root. From slide 1541, × 12.

Fig. 23. Enlargement of central portion of one of the three branches at a slightly higher point: *a*, triangular protostele. From slide 1542, × 75.

Explanation of Plate

PLATE 16

Sphenophyllum plurifoliatum

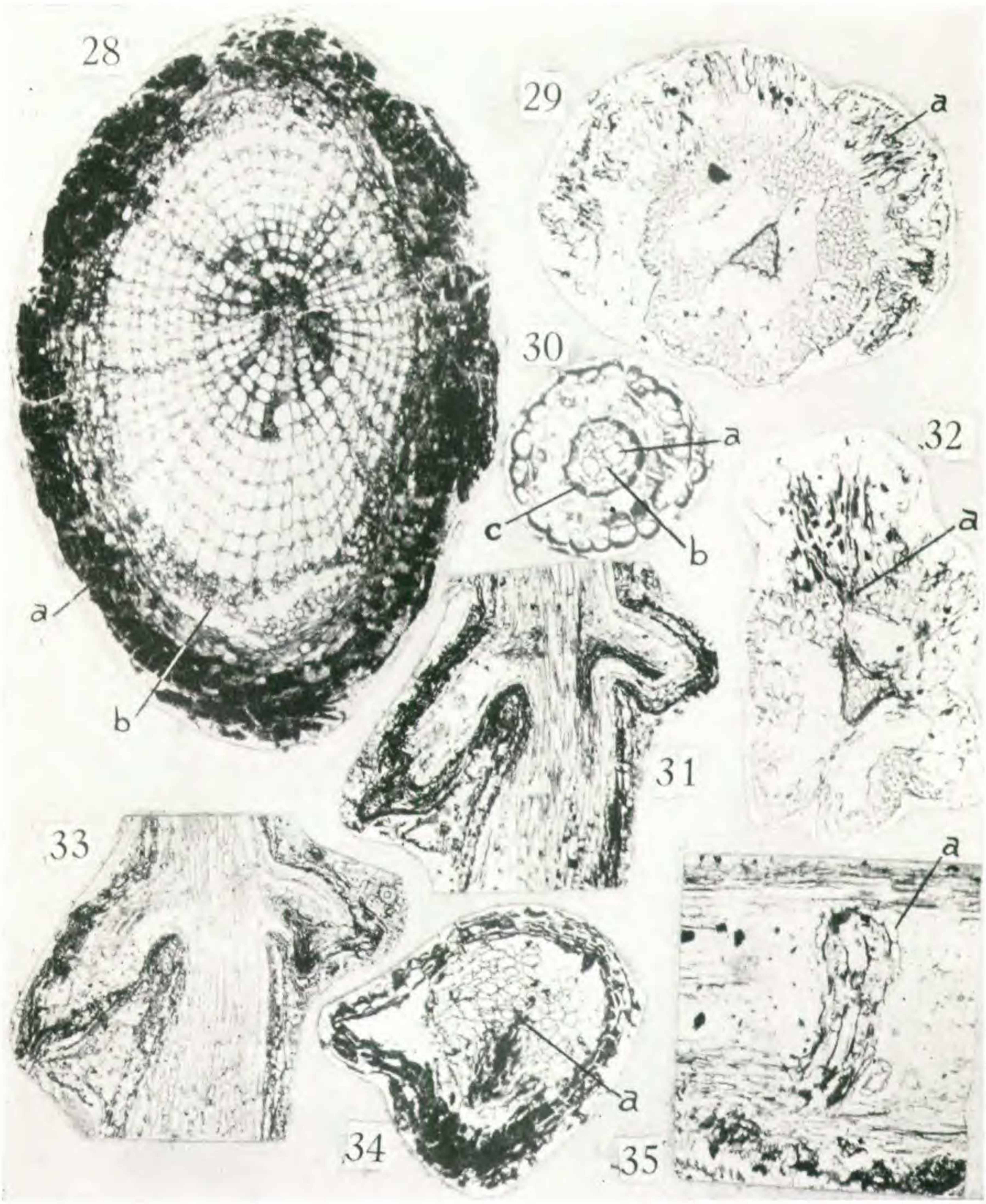
Fig. 24. Segment of a *Sphenophyllum* leaf showing conspicuous dark fiber ring surrounding small elements of vein. From slide 1543, × 120.

Fig. 25. Transverse section of a stem showing branching: *a*, root branching; *b*, modified adventitious root; *c*, large bundle of fascicular wood coming off into side branch. From slide 1544, × 22.

Fig. 26. Same stem as in fig. 25 at higher point of branch departure: *a*, vascular bundle shown in fig. 25 *(c)* now separated from the central stele. From slide 1545, × 22.

Fig. 27. Transverse section of a small stem at a node with portions of its six leaves surrounding it. From slide 1546, × 26.

BAXTER—*SPHENOPHYLLUM PLURIFOLIATUM*



BAXTER—*SPHENOPHYLLUM PLURIFOLIATUM*

Explanation of Plate

PLATE 17

Sphenophyllum plurifoliatum

Fig. 28. Transverse section of a large root: *a*, periderm; *b*, phloem. From slide 1547, × 20.

Fig. 29. Transverse section of a stem at a node showing fused whorl of leaves: *a*, leaf base. From slide 1546, × 24.

Fig. 30. Transverse section of a small root: *a*, secondary xylem; *b*, protoxylem; *c*, endodermis. From slide 1526, × 45.

Fig. 31. Longitudinal section of a stem with large branching roots. Note horizontal passage of vascular tissue into right-hand root. From slide 1548, × 15.

Fig. 32. Transverse section of a small stem at node: *a*, V-shaped leaf traces shown pulled away from the protoxylem angle of the stele. From slide 1546, × 24.

Fig. 33. Same stem as in fig. 31, showing branching of small roots from one of the large roots. From slide 1534, × 15.

Fig. 34. Transverse section of small root showing endogenous origin of branch root: *a*, protoxylem. From slide 1549, × 30.

Fig. 35. Longitudinal section through the middle cortex of a stem showing an adventitious root in both transverse and longitudinal view: *a*, characteristic large epidermal cells. From slide 1550, × 23.